Buchenavia capitata (Vahl) Eichl. Granadillo

Combretaceae Combretum Family

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Buchenavia capitata (Vahl) Eichl., commonly known as granadillo, is a large tree with a straight trunk bearing a few, widely spreading, nearly horizontal branches with thin foliage. The small, spoon shaped (spatulate), yellow-green leaves are borne in upright clusters crowded at the ends of short erect twigs. Mature trees in Puerto Rico reach 20 to 25 m in height and 0.7 to 1.3 m in d.b.h. In Trinidad, trees grow to a 35-m height (*26*). Because of its attractive form, granadillo has been used as an ornamental.

HABITAT

Native Range

Granadillo grows naturally from 23° N. to 23° S. latitude in the neotropics, a range defined approximately by the cities of Havana, Cuba, and Rio de Janeiro, Brazil (fig. 1). It is reported as native to Cuba (*35*), including the Isle of Pines (*2*); Jamaica (*1, 37, 38*); Hispaniola (*34*); Puerto Rico; Tortola; the Lesser Antilles; Trinidad and Tobago (*4, 5, 26*); Panama (*48*); and South America, from Venezuela (*15, 29*), Suriname (*30*), and French Guiana (*17*), the south to Brazil and Bolivia (*22*). Granadillo has also been introduced as a shade tree in southern Florida, where it is reported to be hardy (*22*).

Climate

In Puerto Rico, granadillo grows in the subtropical moist, subtropical wet, and subtropical rain forest life zones (*16*), where it is a relatively uncommon tree. Mean annual precipitation in these areas ranges from 1500 to nearly 4000 mm. Mean annual temperatures range from 22 to 24 °C with little variation during the year (*8*). Throughout the remainder of its natural range, mean annual rainfall and temperature do not deviate greatly from the values cited above. Granadillo is native to frost-free regions.

Soils and Topography

In Trinidad, granadillo tolerates "a fair amount of soil moisture" and grows on a variety of soils ranging from sands to clays (*26*). In Jamaica, it grows in the limestone hills (*19*) and in savanna woodlands and thickets with clay soils (*1*).

Granadillo in Puerto Rico's Luquillo Mountains is frequently encountered on gentle to moderate midslopes and upper slopes (*10*) and along ridges, where it is easily identified by its spreading crown. The Luquillo Mountain soils are principally ultisols and inceptisols derived from igneous rocks. Granadillo is also reported on clay soils derived from limestone in north-central Puerto Rico (*22*). Granadillo planted in southern Florida grows satisfactorily on dry soils and in exposed sites (*22*).

Associated Forest Cover

Granadillo appears to be an infrequent component of tropical moist and subtropical moist forests in Holdridge's (*21*) life zone classification system. It is also found in premontane moist forests and subtropical wet and rain forests, although there is some evidence that it favors drier sites (*18, 20*). In Beard's (*5*) classification system, granadillo is found in the evergreen seasonal, the semievergreen seasonal, and the lower montane rain forests.

Figure 1—*Range of granadillo* (Buchenavia capitata) *in the New World.*

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At the time of Puerto Rico's discovery, granadillo grew in forests of the coastal lowlands through the mountainous interior (*22*). The original forests, with trees that probably reached a 35-m height, contained about 170 tree species (*41*). Today, after extensive land clearing for agriculture, granadillo is an infrequent component of secondary stands in Puerto Rico's central mountains (*45*). Granadillo was also observed on leeward slopes in Dominica's secondary evergreen or semievergreen forests, at an elevation of about 300 m (*20*), and in secondary forests on St. Lucia and Grenada (*5*).

Tree species associated with granadillo are indicated in table 1. Biomass sampling at lower elevations in Puerto Rico's Luquillo Mountains revealed that granadillo's horizontal branches supported abundant loads of epiphytes (*28*). On the Isle of Pines, Cuba, the branches of granadillo are covered with an epiphyte identified as *Tillandsia usneoides* (*2*).

LIFE HISTORY

Reproduction and Early Growth

Flowering and Fruiting.—Granadillo bears numerous small greenish flowers, each about 0.3 cm in diameter, at the end of a lateral stalk which measures over 3.0 cm long (*22*). Flower clusters (spikes) are 1.3 to 2.0 cm long and inconspicuous among the leaves. The clusters bear crowded, hairy flowers that are bisexual or male (polygamous). The calyx is broadly cup shaped, contains five teeth, and measures about 0.15 cm in length. There are 10 stamens and an inferior 1-celled ovary. Honeybees are the most frequent pollinators (*33*). Elliptical, greenish fruits, about 2 cm in length and 1.2 cm in diameter, are borne singly or in pairs.

In Puerto Rico, granadillo drops all of its leaves in April and May, at the time of its annual flowering (*14*). This follows a period of reduced rainfall lasting from mid-January through mid-April. Leaf fall occurs earlier and more rapidly on dry sites than wet sites, probably in response to decreased moisture (*33*). The fruits are drupes, about 2 cm in length and 1.2 cm in diameter, which mature and fall along with the leaves at the time of annual flowering (*14*). In Trinidad, granadillo flowers and develops new leaves in April, and the fruit matures in December (*26*).

Seed Production and Dissemination.—Granadillo seeds are difficult to collect because only a few of the trees bear fruits in a particular year, and there is an extended period of time between crops for individual trees (*49*). Some of the fruits serve as a food source for the Puerto Rican parrot, *Amazon vittata*. Most of the fruits, however, fall within 4 m of the parent tree and are decomposed by microorganisms or eaten by insects (*33*). The absence of native mammals and large birds within the Luquillo Forest may partially account for the lack of dispersion of the seeds.

Tests conducted at the Institute of Tropical Forestry in Rio Piedras, PR, revealed that there were averages of 295 fruits per kilogram and 760 seeds per kilogram (*49*). Of 148 granadillo fruits tested in Puerto Rico, 28 percent had fully developed seeds, and the remainder were empty or not viable (*49*). Much of this damage may be attributable to insect infestation. After field collection, most of the empty fruits can be separated from the sound ones by a flotation test. This test sometimes yields poor results when used with fresh fruit having a fleshy exocarp because empty seeds may sink along with the sound ones.

In one seed storage trial conducted in Puerto Rico, seeds planted immediately after collection showed a 62-percent germination. Seeds stored in unsealed paper sacks, at both ambient temperatures and cold storage (4 °C), gave the following germination results, respectively: 1 month storage, 60 and 10 percent; 2 months, 54 and 6 percent; and 3 months, 53 and 2 percent. After 3 months of cold storage, no seeds germinated. Seeds stored at ambient temperature showed 42-percent germination after 6 months of storage, and 32-percent after 9 months. No seeds germinated after 1 year of storage (*49*).

Seedling Development.—Germination is epigeous with the cotyledons rising to about 5 cm above the ground. In Puerto Rico, germination in the Luquillo Forest was observed during the dry season after granadillo leaves had fallen (*33*). During this period, the increased sunlight reaching the forest floor under parent trees enhances germination and the survival of seedlings.

In Trinidad, germination was reported from 6 to 10 weeks after the sowing of seeds (*26*). Seedlings were successfully moved either with bare roots or with a ball of earth. For economic reasons, it was suggested that root and shoot cuttings merited trials (*26*).

In Puerto Rico, the reported average lapse of time between sowing and germination was 10 weeks (*25*). Although observations were not conclusive, it was suspected that more rapid germination would take place if seeds were sown before, rather than during, the dry season. In the forest, 70 percent of undamaged seeds were estimated to germinate (*33*). Seedling density was highest in July but then declined because of mortality, most likely due to competition.

In Puerto Rico, seedlings grew more rapidly in forest clearings than under the canopy (*33*). In contrast, growth of seedlings 8 months after planting in the nursery was more rapid under shade than under direct sunlight. Rapid initial growth was reported in Trinidad, where seedlings grew as much as 1.2 m in 6 months and up to 2.4 m in 1 year (*26*). Puerto Rican planting trials showed slow initial growth on most sites, but then fair to good survival (*49*). One trial of 400 seedlings planted in forest openings resulted in 38-percent survival after 5 years and an average height growth only 0.6 m/yr. The best survival in Puerto Rico was attained when seedlings about 1 cm in diameter and 0.4 to 0.6 m in height were cut back to 15- and 30-cm heights before planting (*49*).

Vegetative Reproduction.—Granadillo coppices freely even at an advanced age (*26, 49*).

Sapling and Pole Stage to Maturity

Growth and Yield.—Growth data for granadillo in the neotropics are sparse. Granadillo's early growth was reported as rapid in Trinidad (*26*), where the species develops large buttresses when mature. Stems averaged nearly a 7-m height in 3 years, with the largest trees growing to 9 m when left in the nursery beds. When transplanted under light shade, the average seedling after 3 years reached 4.5 m in height with the largest trees growing up to 6 m. After 7 years (6 years after transplanting), the largest tree mea-

Table 1.—*Associated forest cover of major tree species with granadillo* (Buchenavia capitata)

Country	Locality	Elevation	Rainfall	Principal associated species and ecological information*	Source
		m	*mm/yr*		
Puerto Rico	Central Mountains	150–600	1500–2500	*Tabebuia heterophylla, Andira inermis, Inga vera* in abandoned coffee shade forests > 30 years old.	*(45)*
	Central Mountains	150–1100	1500–2500	*Dacryodes excelsa, Manilkara bidentata, Sloanea berteriana*	*(40, 41)*
	Luquillo Mountains	150–600	2000–3000	*Dacryodes excelsa, Euterpe globosa, Sloanea berteriana;* granadillo is ranked 27th in stem density, 8th in basal area dominance and seventh in volume on meaasured plots	*(6)*
		~300	~3000	*Dacryodes excelsa, Euterpe globosa, Micropholis garciniaefolia;* granadillo constituted 0.2 percent of stems in undisturbed tabonuco forest	*(42)*
		180–360	2300	*Manilkara bidenta* on upper slopes; granadillo is a secondary species on gentle to moderate slopes	*(10)*
	University of Puerto Rico Experiment Station	~50	1500	*Phoebe elongata, Guarea trichilloides, Inga laurina* in secondary woodlots	*(46)*
Cuba	Sierra Maestra region	150–900	3200	*Andira inermis, Calophyllum brasilense, Prunus occidentalis* on north slopes	*(35)*
	Cabo Cruz region	~150	...	*Andira inermis, Bursera simaruba, Cedrela mexicana;* soils with limestone surface layer	*(35)*
	Orient region (several sites)	150–370	~3000	*Carapa guianensis, Ficus membranaceae, Guarea guara;* soils of igneous origin	*(35)*
	Pinar del Rio	360	~1500	*Andira inermis, Calophyllum brasilense, Guarea guara;* soils derived from limestone	*(35)*
	Trinidad Mountains	450	>2000	*Cedrela mexicana, Phoebe elongata, Zanthoxylum martinicense*	*(35)*
Trinidad	Evergreen seasonal forest	<300	1800–3000	*Carapa guianensis-Eschweilera subglandulosa* association; granadillo is ranked eighth or ninth in stem density in three faciations as an emergent tree	*(4)*
	Semievergreen seasonal forest	lower slopes	<1500	*Peltogyne porphyrocardia* association; in the *Protium guianense-Tabebuia serratifolia* faciation, granadillo occurred as an upper story tree and ranked sixth in stem density	*(4)*
	Deciduous mountainous seasonal forest		1100–1500	*Bursera simaruba-Lonchocarpus punctatus* association; granadillo ranked 12th in stem density as an emergent tree	*(4)*
	Lower montane forest	≤600	>2500	*Byrsonima spicata-Licania ternatensis* association; granadillo ranked sixth in stem density as a canopy tree	*(4)*
St. Kitts-Nevis	Lower montane forest	>400	>2000	*Dacryodes excelsa-Sloanea* spp. association	*(4)*
St. Lucia	East coast near Praslin	~100	–1500	Myrtaceae species, *Bursera simaruba,* and *Pimenta racemosa* on secondary woodlands	*(4)*
Grenada	Morne Delice	230–340	–2000	*Manilkara bidentata, Carapa guianensis,* and *Chione venosa* in late secondary seasonal forests	*(4)*

* Nomenclature according to cited authors.

sured 10.5 cm in d.b.h. and 10.7 m in height. The average of the 10 best trees was 9.7 cm in d.b.h. and 9.3 m in height. The largest of 200 saplings planted on an open, degraded site at an 800-m elevation in Puerto Rico's Toro Negro Forest averaged only 0.5 m/yr during 6 years (table 2). This slow growth on the Toro Negro Forest may be attributed to the comparatively high elevation and the degraded condition of the site.

The d.b.h. growth of granadillo trees on several permanent plots in the Luquillo Mountains is summarized in table 2. The lowest values, those averaging between 0.05 and 0.51 cm/yr reported for the TS-3 and TR-1 permanent plots, highlight the variability in increment for scattered stems of different sizes in undisturbed primary stands. In contrast, granadillo's d.b.h. growth in the Sabana 8 and Rio Grande advanced secondary stands, both of which had been thinned, averaged about 0.70 cm/yr. Granadillo, throughout most of its life cycle, is one of the fastest growing species in the subtropical wet forest of the Luquillo Mountains (*11, 43*).

A survival curve and life table were devised for granadillo

Table 2.—*Growth information for granadillo* (Buchenavia capitata) *in Puerto Rico*

Locality	Elevation	Rainfall	Duration	Mean growth		Comments	Source
				Height	D.b.h.		
	m	*mm/yr*	*Years*	*m/yr*	*cm/yr*		
Toro Negro Forest	~800	~2500	6	0.50	0.80	Measurement was of largest sapling of 200 planted on open, degraded site.	*(24)*
Luquillo Mountains	~250	~2500	2	...*	0.66	Average diameter growth of 15 trees	*(43)* *(39)*
	180–600	2300–3500	18	...	0.70	Average for 30 trees from Sabana 8 site and 11 trees for Rio Grande site	*(11)*
	570	~3000	3	...	0.05	Average for two trees from TS-3 plot in a climax forest	*(44)*
	400	~3500	30	...	0.51	Average for four trees from TR-1 plot in a climax forest	*(44)*

* Information not given in columns or rows is not available.

using data collected on the Luquillo Forest of Puerto Rico for trees of different sizes (*33*). For every 1,000,000 seeds produced, 1,000 germinate, 200 develop into seedlings during the first couple of years, 60 grow to saplings after 7 years, 40 develop into mature trees after 30 years, and about 30 reach senescence at 40 to 70 years. Mortality rates in the seedling and juvenile size classes are high.

Rooting Habit.—The seedling develops a taproot rapidly (*26*). The roots of mature trees, however, appear to be fairly close to the soil surface. Endotrophic mycorrhizae, believed to act as nutrient traps, have been identified in association with granadillo roots (*12*).

Reaction to Competition.—Granadillo is intolerant of shade (*26*). In Trinidad, natural regeneration was reported as poor in closed forests and only sparse in forest openings where light was adequate. Moreover, smaller diameter classes were not well represented in the forest. These observations were confirmed on a 0.54-ha sample plot in Puerto Rico's undisturbed subtropical wet forest (*33*). After grouping the stems on this plot into 5-cm classes ranging from 10 to 100 cm, disproportionately greater numbers of stems were found between the 30- and 60-cm classes. This type of diameter class distribution usually characterizes a tree species that reproduces in forest gaps caused by recurrent disturbances such as high winds or hurricanes. In another Puerto Rican study, granadillo was classed as a secondary forest canopy species mainly because of the paucity of seedlings and understory stems represented (*36*). Several other characteristics of granadillo suggest that it is a late secondary species: fruits dispersed by gravity; wide crown; deciduous habit, even in areas of heavy rainfall; considerable mortality in early stages; and a rapid growth rate (*4, 7, 33*).

Biomass sampling of Puerto Rico's Luquillo Forest included three granadillo trees with d.b.h.'s ranging from 3.1 to 20.6 cm. Biomass estimates of granadillo's leaves, branches, trunks, roots, and attached epiphytes are reported in table 3. Major chemical components of granadillo roots, boles, branches, and leaves are summarized in table 4.

Damaging Agents.—Rats, introduced to Puerto Rico some time ago, are found within the Luquillo Forest, where they collect granadillo seeds, store them in small caches, and then split the endocarps and eat the embryos (*33*). Native insects also consume the seeds (*33*).

Granadillo heartwood is fairly resistant to decay and to attack by aboveground nesting termites (*Nasutitermes* spp.) and very resistant to attack by the subterranean, or drywood termite (*Crypotermes brevis* Walker), but it exhibits little resistance to marine borers (*9, 13, 47*). The sapwood is vulnerable to powder-post beetle attack. The heartwood is impermeable, and penetration of the sapwood with oil- or water-based preservatives is very low.

Granadillo has been shown to be susceptible to hurricanes in Puerto Rico. Hurricane San Felipe of September 1928 caused breakage of tree tops, and about 2 months elapsed before the crowns refoliated (*3*). Hurricane Hugo, a September 1989 storm, also caused damage to granadillo crowns, especially in the northeastern part of the Luquillo Forest. Refoliation occurred within 2 to 3 months.

SPECIAL USES

The wood of granadillo shares many characteristics with the wood of white oak and teak (*9*). The heartwood is yellowish brown and not easily separated from the pale yellow-brown sapwood (*23*). The wood is medium to rather coarse in texture, has a high luster, and a specific gravity of 0.63 g/cm^3. The lumber air-seasons rapidly to a moisture content of 15 percent with only a small amount of degrade. The percentage of shrinkage from green to ovendry is 2.8 radial, 5.7 tangential, and 8.6 volumetric (*9*). The wood machines with moderate difficulty because of its hardness, although planing, shaping, turning, boring, mortising, sanding, and resistance to screw spliting are considered good (*22*). The wood finishes well and takes an attractive satiny polish. The bark is high in tannin (*22*).

Granadillo's uniform color, attractiveness, and good machining properties make it highly suitable for furniture and cabinetwork (*22, 23, 31, 32, 38*). It may also be used for construction, framing, flooring, plywood, decorative veneer, interior trim, boat building, boxes, crates, wood tanks, and turnery (*9, 22, 23*). Granadillo has also been recommended as an ornamental for planting along roadsides because of its attractive form (*27*).

Table 3.—*Biomass estimates for granadillo* Buchenavia capitata *in Puerto Rico (28)*

Tree dimensions		Oven-dry weight					
D.b.h.	Height	Leaves	Branches	Bole	Roots	Total	Epiphytes
cm	*m*	*kg*					
3.1	5.71	50	143	1,327	391	1,911	30.5
5.6	10.98	279	456	7,147	1,094	9,003	26.1
21.6	19.89	2,698	8,238	213,725*	100,042	324,703*	1596.7

* Values are altered from those reported in *28*. The original data appear to be about 10 times too high due, perhaps, to a rounding error.

Table 4.—*Major chemical components of granadillo* (Buchenavia capitata) *in Puerto Rico (28)*

Tree Component	Element					
	Na	K	Ca	Mg	P	N
	Range in percentage of ovendry weight					
Roots						
Small	0.01–0.03	0.09–0.13	0.46–0.75	0.08–0.13	0.019–0.025	0.39–0.60
Medium and large	0.01	0.09–0.14	0.34–0.60	0.03–0.06	0.017–0.025	0.26–0.39
Butt	....*	0.09–0.50	0.21–0.44	0.03–0.14	0.013–0.027	0.23–0.32
Boles	....	0.13–0.20	0.27–0.50	0.03–0.05	0.017–0.024	0.25–0.28
Branches	....	0.24–0.38	0.44–1.33	0.04–0.12	0.024–0.038	0.35–0.69
Leaves	....	0.56–1.84	0.60–1.16	0.14–0.42	0.070–0.140	1.08–2.25

* Information not given in columns or rows is not available.

GENETICS

The genus *Buchenavia,* confined to tropical America, belongs to the subtribe Terminaliinae of the Combretaceae family (*16*). The genus is apparently derived from the *Terminalia,* which is pantropical in distribution. The two genera are distinguished on the basis of filaments and calyx lobes. *Buchenavia capitata* was previously classified as *Bucida capitata* Vahl. (*22*) and as *Terminalia capitata (17, 31).*

Buchenavia is the largest genus of Combretaceae confined to one hemisphere. It contains 22 species, mainly in the Amazon Basin of South America, one of the principal areas of speciation within the family (*18*). *Buchenavia capitata,* by far the most variable, abundant, and widely distributed species in the genus (*17*), is the only species found in the West Indies.

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